



REVIEW PAPER

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Review of radiation interception and radiation use efficiency in intercropping in relation to the analysis of wheat/faba bean intercropping system

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Abstract

Growth and final total yields of crops and intercrops largely depends on the interception and the efficiency of use of growth resources namely water, nutrient and radiation. The literature indicates that provided water and nutrients are not limiting, growth and final yields of crops is mainly dependant on the amount of intercepted photosynthetically active radiation (PAR) and the efficiency of its use by the crops and/or the intercrops (i.e. Radiation use efficiency). However, PAR, which is a free natural resource, must be intercepted and utilized instantaneously, as it cannot be stored for later use. Empirical evidences abounds to indicate that it is possible to improve the interception of PAR by the crop through the manipulation of agronomic tools such as sowing date, seeding rate, fertilization, intercropping amongst others. Wheat (*Triticum aestivum* L.) plus faba bean (*Vicia faba* L.) intercropping system experiments are increasingly being carried out but only a few of these investigations studied PAR interception and RUE. This paper reviews PAR interception, RUE and associated variables with particular emphasises on the need to assess these variables in wheat/faba bean intercrop system.

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Introduction

Solar radiation is a flux of electromagnetic energy, which must be intercepted and utilized instantaneously, as it cannot be stored for later use (Keating and Carberry, 1993; Tsubo *et al.*, 2001). The importance of radiation lies in the vital role it plays in photosynthesis (Monteith, 1972; Sinoquet *et al.*, 2000; Tsubo *et al.*, 2001; Khan *et al.*, 2010). Photosynthesis involves a process in which green plants use radiation, water and nutrients to synthesise organic compounds from inorganic materials (Biscoe and Gallagher, 1978). Radiation also has an important role in water use through effects on evaporation (Keating and Carberry, 1993; Singer *et al.*, 2011) and transpiration (Sinoquet *et al.*, 2000; Kanton and Dennett, 2004). However, not all the incident or global radiation is intercepted by a crop (Gallagher and Biscoe, 1978a; Tsubo *et al.*, 2001). The fraction of the global radiation crop uses is called photosynthetically active radiation (PAR) (Black and Ong, 2000; Rizzalli *et al.*, 2002; Vargas *et al.*, 2002). The PAR wavelength is documented to be within the range of 0.4-0.7 μm (Awal and Ikeda, 2003; Zhang *et al.*, 2008). In most cases, PAR is approximated as 0.5 of the global radiation (Monteith and Unsworth, 1990; Bonhomme, 2000).

The green leaf area index (L), usually expressed as the products of the number of plants per unit of ground area, the number of leaves per plant and the mean area of leaves per plant, determines the size of the intercepting surface for radiation (Gallagher and Biscoe 1978b; Zhang *et al.*, 2008). It is important to note that the L together with the angular arrangement of individual leaves determines the amount of radiation that penetrates the canopy and strikes the ground (Tsubo and Walker, 2002; Kiniry *et al.*, 2005; Carretero *et al.*, 2010). This clearly indicates the importance of taking radiation extinction coefficient (k) into consideration whilst the radiation captured by a crop and the efficiency of its use is being determined (Rizzalli *et al.*, 2002; Ruiz and Bertero, 2008; Confalone *et al.*, 2010). Therefore, here an introductory note on k for both

the sole crops and intercrops were given. Nevertheless, Gallagher and Biscoe (1978b) suggested that considering growth in terms of the amount of radiation crops intercepts and/or absorb and the efficiency with which they convert this into dry matter (radiation use efficiency; RUE) may be physiologically more relevant than what were then the traditional growth analysis procedures. Indeed, for many purposes, it would be sufficient to explain yields by the amount of radiation intercepted and/or absorbed as well as the efficiency of the conversion of radiation (Black and Ong, 2000; Vargas *et al.*, 2002; Ruiz and Bertero, 2008). However, it should be pointed out that such analysis is most relevant when using the final biomass yields (Awal and Ikeda, 2003; Carretero *et al.*, 2010) because seed yields may not be a constant fraction of the final biomass yields (Biscoe and Gallagher, 1977; Tsubo *et al.*, 2001; Kiniry *et al.*, 2005).

Several investigations under both sole cropping (Rizzalli *et al.*, 2002; Vargas *et al.*, 2002; Kiniry *et al.*, 2005; Confalone *et al.*, 2010; Singer *et al.*, 2011) and intercropping (Harris *et al.*, 1987; Rodrigo *et al.*, 2001; Tsubo and Walker, 2002; Awal *et al.*, 2006; Zhang *et al.*, 2008) conditions have investigated both the interception of radiation and RUE. In general, the wider literature indicate that in regions where water does not pose critical constraints during the growing period for any given crop species, and the crop is well supplied with growth nutrients mainly nitrogen, productivity is mainly governed by the amount of radiation intercepted and the efficiency of its use by the crops (Harris, 1990; Black and Ong, 2000; Lecoeur and Ney, 2003; Carretero *et al.*, 2010). However, in some areas particularly in the tropics except under irrigated conditions productivity is mostly determined by the amount of water use and water use efficiency (Black and Ong, 2000; Azam-Ali and Squire, 2002; Steduto and Albrizio, 2005; Jahansooz *et al.*, 2007). This is because in these areas irradiance does not appear to be in limited supply during the growing seasons whilst water may

be the major limitation (Bunting, 1974; Collino *et al.*, 2001).

Wheat (*Triticum aestivum* L.) /faba bean (*Vicia faba* L.; henceforth referred to as bean) intercropping system, even though not widely adopted appears to be restricted to areas with cold temperature conditions, where water does not pose many problems to the productivity of these crops and other crops (Harris, 1990; Bulson *et al.*, 1997; Haymes and Lee, 1999; Confalone *et al.*, 2010). In other words, conclusions may be drawn that the productivity of this intercrop combinations is largely determined by the amount of intercepted PAR and RUE. However, as reviewed here only a few investigations on this intercrop combination (e.g Haymes and Lee, 1999) have assessed these variables despite increasing attention given by investigators on other intercrop combinations and sole crops in assessing these important determinants of yields.

Radiation extinction coefficient

The canopy radiation extinction coefficient (k) can be defined as the average projection of leaves onto a horizontal surface (Awal *et al.*, 2006). There has been reports that k quantifies the effectiveness with which a crop canopy of a given L intercepts radiation (Robertson *et al.*, 2001; Kiniry *et al.*, 2005; Carretero *et al.*, 2010). Perhaps this is because k is the most critical element of Beer's law (Donald, 1963; Vandermeer, 1989; Tsubo and Walker, 2002), and is largely a function of the area and form of the leaf, the leaf inclination, the zenith angle of the sun and the leaf azimuth (Awal *et al.*, 2006). In other words, k is a function of leaf angle, solar elevation and leaf transmission coefficient (Monteith, 1965; 1969). Thus, the fraction of incident radiation (I/I_0) transmitted through a crop canopy of thin layers of randomly or non-randomly distributed leaves are considered to decrease exponentially, vertically downwards (Tsubo and Walker, 2002; Kiniry *et al.*, 2005). The Monsi and Saeki (1953) equation (Equation 1) as cited by Donald (1963) describe the

relationship for the extinction of light down a crop canopy.

$$\frac{I}{I_0} = e^{-kL} \quad 1$$

Where I_0 is the incident radiation above the crop canopy, I is the transmitted radiation at a level within the canopy below a leaf area index (L), and k is an extinction coefficient for radiation (Sinoquet *et al.*, 2000).

The equation assumes that the canopy is a homogeneous medium whose leaves are randomly distributed (Black and Ong, 2000; Tsubo and Walker, 2002). Thus, it is assumed that there is no effect of row geometry or clumping on the pattern of light transmission through the canopy (Sinoquet *et al.*, 2000; Azam-Ali and Squire, 2002). In such cases, light transmission obeys Beer's law of exponential decay (Donald, 1963; Vandermeer, 1989; Hongo, 1995) as defined by Equation 2 if Equation 1 is rewritten (Sinoquet *et al.*, 2000). Indeed, the significance of k is that if the radiation transmitted through the canopy follows Beer's law, intercepted radiation by the crop can be calculated from knowledge of L (Monteith, 1965; Yoshida, 1972; Tsubo and Walker, 2002; Shearman *et al.*, 2005).

$$I = I_0 e^{-kL} \quad 2$$

Where all parameters in Equation 2 are as defined in Equation 1 above.

Reports indicate that k value is specific to crop type and stage of development depending upon mean leaf angle and solar angle (O'Connell *et al.*, 2004). Values of k have been found to depend on L (e.g. Carretero *et al.*, 2010) with higher k values tending to be associated with lower L values and vice versa (Awal *et al.*, 2006). Crops with narrow, erect leaves tend to have lower values of k than crops with more horizontally displayed leaf arrangements (Kiniry *et al.*, 2005; Carretero *et al.*, 2010). Indeed, Kiniry *et al.* (2005) suggested that reduced k values (more upright leaves) allows the penetration of better light

into the canopy thereby illuminating more leaf area at a lower intensity of PAR. This invariably causes the canopy carbon exchange rates to increase. Consequently, the RUE may be increased when the biomass is source-limited. Under sole cropping conditions, Stutzel and Aufhammer (1991) reported k values of bean in the range 0.74-0.99. Recently, Confalone *et al.* (2010) also reported k values for bean in the range 0.63-0.81. Similarly, the k value for wheat is in the range of 0.40-0.70 (Azam-Ali *et al.*, 1994 cited in Azam-Ali and Squire, 2002). Indeed recently, wheat k values in the range 0.45-0.75 were found (Carretero *et al.*, 2010).

Radiation extinction coefficient in intercropping

Largely most models of light distribution within a canopy are based on Beer's law and there has been several attempts at extending it to intercropping (Sinoquet *et al.* 2000; Tsubo and Walker, 2002; Awal *et al.* 2006). Ong *et al.* (1996), as cited by Azam-Ali and Squire (2002), stated that the canopy structure could be considered as horizontally homogeneous but vertically heterogeneous. Accordingly, the intercrop canopy can be stratified into several horizontal layers such that light interception by each component in each layer can be calculated following the method described by Keating and Carberry (1993). Indeed, the reader would find the paper by Keating and Carberry (1993) a useful resource to read. These authors assumed that the intercrops are a closer approximation to the randomly distributed leaves required for Beer's law than the sole crops due to greater plant density. Wheat/bean intercrop systems do not exhibit this ideal stratification of canopy to necessitate computation of k values for each component crop in the intercrop (see Hongo, 1995; Haymes and Lee, 1999). It is the opinion of the writer that estimating k value for the whole system may be more relevant. However, it should be pointed out that k value calculated for the whole system might not have much meaningful interpretation, as k is known to be

specific to a given crop species (O'Connell *et al.*, 2004).

Awal *et al.* (2006) asserted that with respect to the less- competitive component crop species in the intercrop, the use of the same k values for both sole and intercrop is misleading. This is because the canopy structure of the dominated component is usually different from that of its sole crop (see Keating and Carberry, 1993). They reiterated that k values computed from Beer's law may provide accurate estimates of the radiation intercepted by a sole crop or by the dominant crop in an intercrop that receives uniform direct solar radiation. However, according to them it would not provide accurate measures of k or thorough prediction of light interception for the dominated crop species that experiences mostly diffused radiation (see Monteith and Unsworth, 1990). Indeed, the k values of the dominated component crop species depends not only on its own canopy architecture and its radiation attributes, but may also depend on some of the architectural and radiation characteristics of the dominant crop canopy (Awal *et al.*, 2006).

The interception of radiation by crops

The literature indicate that the total incident PAR onto a given crop canopy is a function of location, year, sowing date and crop phenology (Ruiz and Bertero, 2008). On the other hand, the fraction of the incident PAR intercepted by a given crop canopy is a function of L and k (Collino *et al.*, 2001; Ruiz and Bertero, 2008; Confalone *et al.*, 2010). A vast majority of the literature indicates that early in crop growth and development, light interception largely depends upon how fast leaves are formed and expand (Yoshida, 1972; Gallagher and Biscoe 1978b; Rodrigo *et al.*, 2001). Moreover, the size and duration of leaves also determine the rate and duration of dry matter accumulation (Carretero *et al.*, 2010). As pointed out in the introductory section, L determines the size of the intercepting surface (Gallagher and Biscoe 1978b). Indeed the L and the angular arrangement of individual leave determine the

amount of radiation that penetrates the canopy and strikes the ground. It is therefore not surprising that k is the most important element in Beers' law (Carretero *et al.*, 2010).

It is clear that for incident (global) radiation above a crop canopy (I_o), if the transmitted value at the bottom of a canopy is (t), the difference between the incoming and transmitted (I_o-t) is termed as intercepted radiation (I) (Sinclair and Muchow, 1999; Tsubo *et al.*, 2001; Awal and Ikeda, 2003). The intercepted radiation in turn has two major components, the absorbed radiation (ar) and reflected radiation (rr). The difference between the radiation intercepted and reflected by the crop is termed the radiation absorbed (Gallagher and Biscoe, 1978a; Awal and Ikeda, 2003). In most cases for closed canopies, about 6% of the intercepted radiation is reflected back to the atmosphere. However, due to the technical difficulties in measuring the quantity absorbed most studies usually present data on the quantity intercepted (Gallagher and Biscoe, 1978a; Singer *et al.*, 2011). This is because in most cases reflected radiation is not measured. Hence, absorbed radiation cannot be estimated with precisions. In such cases productivity are usually evaluated based on the intercepted radiation

Nowadays, most measurement of radiations is in the form of PAR rather than total radiation (e.g. O'Connell *et al.*, 2004; Carretero *et al.*, 2010). Thus, radiation measurements are usually carried out using ceptometers that measures PAR rather than solarimeters, which is mostly based on total or global radiation (see Haymes and Lee, 1999). Indeed, it is possible to calculate cumulative PAR by the crop from sowing to any given period (Giunta *et al.*, 2009; Carretero *et al.*, 2010; Singer *et al.*, 2011). For instance, it has been demonstrated that logistic curves can be fitted to percentage light interception multiplied by the thermal time (base temperature = 0°C) on a per plot basis to derive fractional interception per day (Kindred and Gooding, 2005;

Giunta *et al.*, 2009). These authors reported that subsequently, the estimates were combined with daily radiation receipt data to calculate the total amount of PAR intercepted per day and then over the life of the crop. The procedures involved can be simply stated as follows.

First, the proportion of intercepted PAR by the canopy, usually called radiation interception efficiency (RIE) (Ruiz and Bertero, 2008; Carretero *et al.*, 2010) is calculated as the ratio between the difference of incident PAR (i.e. PAR above the canopy) and transmitted PAR (i.e. PAR below the canopy) to the incident PAR (PAR above the canopy)

$$RIE = \left(\frac{I_o - t}{I_o} \right) \quad 3$$

Where I_o and t refers to PAR above (incident PAR) and below (transmitted PAR) the canopy respectively.

Thereafter, logistic curve are usually fitted to the mean values of the RIE x thermal time (tt) (accumulated from sowing until a given period) for each plot to derive fractional PAR intercepted per day (PAR_f) using Equation 4

$$PAR_f = \frac{c}{1 + e^{(-bx(tt-m))}} \quad 4$$

Where c = maximum PAR intercepted, m = tt at 50 % of the maximum PAR interception and b = logistic rate scalar for light interception.

Finally, these values (i.e. PAR_f) are usually multiplied with the daily incident (global) radiation recorded at the automotive weather station in the experimental field to calculate the total amount of PAR intercepted per day (PAR_d) and then over the life of the crop. That is the cumulative or total intercepted PAR (PAR_c) (Giunta *et al.*, 2009). However, in most cases global radiation received are measured using solarimeters not ceptometers. In such cases there would be need to make conversion to PAR. Giunta *et al.* (2009) in their study converted the daily total radiation receipt to PAR by multiplying by 0.5 (Monteith, 1972; Monteith and

Unsworth, 1990). Several workers (Gooding *et al.*, 2002; Kindred and Gooding, 2005; Jahansooz *et al.*, 2007) have also used similar procedures. To my knowledge this procedure has rarely been used in assessing intercepted radiation in wheat/bean intercropping system. Indeed whilst light measurements have been previously carried out in wheat/bean intercropping system (e.g. Hongo, 1995; Haymes and Lee, 1999), the approaches used were slightly dissimilar to the methods illustrated above. It is worthy to state that at maximum canopy development, it has been demonstrated that sole wheat intercepted significantly less light (85%) than both sole bean and the intercrop (94% each) (Haymes and Lee, 1999). However, it should be pointed out that this investigation gave only limited indications of light interception by the two crop combinations, as light were not assessed in all the experiments they reported.

Whilst the procedure discussed earlier as regards the interception of light is simple and has been used mostly in sole cropping conditions, it has not been widely applied under intercropping conditions. However, it should be pointed out that this is not the only method for measuring light interception by a crop even though other investigators have used similar approaches (Lecoecur and Ney, 2003). It would interest the reader that one of the advantage of this method is that the need to assess both L and k before calculating light interception is eliminated. In other words, this approach based on data using ceptometer does not only help it easy to take measurements of light above and below the canopy, but the L and invariably k are automatically determined. Whilst the writer acknowledges that there are several other methods of assessing radiation, in this paper other methods were not discussed. Readers are referred to the works of several investigators on light interception such as Rodrigo *et al.* (2001), Tsubo and Walker (2002), Awal and Ikeda (2003), Kiniry *et al.* (2005), Awal *et al.* (2006), Zhang *et al.* (2008), Carretero *et al.*

(2010) for sole crops, intercrops or both as may be applicable.

It should be emphasised that light interception by a canopy of leaves is strongly influenced by the leaves size and shape, angle and azimuthal orientation, vertical separation and horizontal arrangement of leaves and by absorption by non-leaf structures (Yoshida, 1972). In other words, L has a large influence on radiation interception by a canopy of crop (Biscoe and Gallagher, 1978; Zhang *et al.*, 2008). Other factors that affect interception include the total amount of global radiation, crop species or variety involved (Awal *et al.*, 2006), crop growth and development stage (Tsubo *et al.*, 2001). The canopy architecture associated with k (Carretero *et al.*, 2010), drought (Collinson *et al.*, 1996; 1997), N content of the foliage (Lemaire and Gastal, 1997 cited in Azam-Ali and Squire, 2002), temperature (Confalone *et al.*, 2010) and foliar diseases (Carretero *et al.*, 2010) also affects the amount of radiation intercepted.

Interception of radiation in intercropping

Keating and Carberry (1993) stated that the productivity per unit incident radiation might be improved by the adoption of a cropping system that either increases the interception of radiation and/or maintains higher radiation use efficiency. There have been several suggestions of ideal leaf orientation in order to improve the capture of radiation by the sole crop (Yoshida, 1972; Azam-Ali and Squire, 2002). Intercropping is one of the sustainable ways to improve the interception of radiation by a crop particularly during the early stages of growth (Harris, 1990; Awal *et al.*, 2006; Jahansooz *et al.*, 2007). From the top to the bottom of a crop canopy, light available for photosynthesis diminishes such that at some levels the amount of light falls below the crop's compensation point, suggesting that a crop with a lower compensation point could be put in. Vandermeer (1989) stated that in some cases, it would be necessary to introduce the second species at a specific level, even though the first crop species has

not yet reached its compensation point, to improve the overall productivity of the whole system. The additional radiation captured by the intercrop canopy facilitates greater dry matter accumulation and may lead to more seed yields (Rodrigo *et al.*, 2001; Awal *et al.*, 2006; Zhang *et al.*, 2008).

For the intercrop, there are two basic principles involved if light interception were to be improved. Largely, the amount of radiation interception by an intercrop can be improved through temporal and/or spatial manipulation of agronomic practices (Marshall and Willey, 1983; Francis, 1989; Awal *et al.*, 2006; Zhang *et al.*, 2007; 2008). Details on each of these principles are discussed in a subsequent section of this paper. However, it has been asserted that intercrop may not supersede the component sole crops with respect to radiation interception, unless the planting density of the latter is below the optimum (Azam-Ali and Squire, 2002). From the available evidences in the literature regarding greater interception of radiation by intercropping (Marshall and Willey, 1983; Harris *et al.*, 1987; Awal *et al.*, 2006; Zhang *et al.*, 2008), this writer begs to take a contradictory stand.

Improving radiation interception by spatial complementarity between the component crop species

Spatial resource use refers to a phenomenon where the intercrops make use of resources at the same time but in differing form due to their morphological and/or phenological attributes (Francis, 1989; Jahansooz *et al.*, 2007; Zhang *et al.*, 2008). Spatial complementarity is possible in situations where there is heterogeneity in the canopy and root systems of intercrops resulting in improved resource utilization (Willey, 1990; Sivakumar, 1993). Willey (1979a) stated that where crop differences results in greater canopy differences, greater improvement in radiation might be possible. This is because at one extreme is the situation in which a taller crop species do not completely utilize the incoming radiation, even when planted at its optimal density. Thus, the light

environment at the ground contains wasted light, which obviously could be used by another crop (Vandermeer, 1989; Harris, 1990). Hence, adding the other crop may not affect light interception by the main component at all yet could increase the radiation use efficiency by increasing the value of the proportional light interception (Vandermeer, 1989). It is likely that earlier yield advantages reported for wheat/bean intercropping system (e.g. Haymes and Lee, 1999) may be due to spatial complementarity in resource use between the two component crops. This is because in most of the studies the two crops were planted and harvested simultaneously, suggesting that any beneficial effects of temporal complementarity in resource use might not have been possible (Bulson *et al.*, 1997).

Nevertheless, with respect to spatial interception of radiation, in sole crops, the idealized pattern of light distribution is described by vertical, or erectophile leaves (i.e. low k values) in the upper-most layers and planophile or horizontal leaves at the bottom of the canopy (Bonhomme, 1993 cited in Azam-Ali and Squire, 2002; Carretero *et al.*, 2010). The aim is to reduce light saturated wasteful leaves on the upper positions and increase light available for non-saturated lower leaves (Reynolds *et al.*, 2009). As regards intercropping, light interception can be improved spatially by decreasing the shading effects of vertically dominant component species if the taller component species has erectophile leaves (Ofori and Stern 1987; Francis, 1989) and isobilateral leaf characteristics of the cereals (Awal *et al.*, 2006) above an understory species with predominantly planophile leaves for instance a seed legume (Azam-Ali and Squire, 2002; Awal *et al.*, 2006). It is usually assumed that erect canopy of the taller species will absorb incident radiation very efficiently without starving the shaded component optimal levels of transmitted radiation (Vandermeer, 1989; Awal *et al.*, 2006). As Azam-Ali and Squire (2002) stated this arrangement can be exemplified by intercrops composed of a tall C_4 species such as millet (*Pennisetum glaucum*), sorghum (*Sorghum bicolor*)

and maize (*Zea mays*), overlying a C₃ legume such as cowpea (*Vigna unguiculata*), or groundnut (*Arachis hypogaea*). In such cases, higher intensities of radiation can be intercepted by the cereal component allowing the penetration of lower intensities that are below the saturation levels for C₃ species. Clearly, with respect to spatial complementarity in radiation, wheat/bean intercrop combinations are clearly not ideal intercrop combinations as regards the utilization of light despite the positive benefits reported earlier for this intercrop combination (e.g. Hongo, 1995).

Improving radiation interception by temporal complementarity between the component crop species

Temporal resource use refers to a phenomenon where the intercrops make use of resource at different times such that competition is less (Willey, 1979b; Francis 1989; Ong *et al.*, 1991 cited in Rodrigo *et al.* 2001; Zhang *et al.*, 2008). Temporal complementarity in resource use is possible when crops of differing durations are grown together, making demand for resources at different times of the growing season (Sivakumar, 1993; Jahansooz *et al.*, 2007; Zhang *et al.*, 2008). For instance, Willey (1990) stated that sorghum /pigeon pea (*Cajanus cajan*) is typical of many satisfactory temporal combinations of intercrops. It combines rapid-growing early maturing sorghum with a slow-growing late-maturing pigeon pea. For this intercrop combination, the presence of sorghum allows for temporal complementary in radiation interception as pigeon pea allows for later interception of light.

It of interest to note that this temporal benefit was exemplified by the higher yield achieved even though sorghum was more competitive than pigeon pea in their investigation (Willey, 1990). Similarly, Zhang *et al.* (2008) recently, concluded that radiation interception increased in wheat/cotton (*Gossypium* spp.) intercrops compared to the sole crops, partially by utilizing PAR during winter and spring by the wheat crop, which could otherwise be wasted when

growing only a sole crop of cotton. Wheat/bean intercrop are usually sown and harvested at the same time (e.g. Bulson *et al.*, 1997; Haymes and Lee, 1999), thus suggesting that with respect to radiation, temporal complementarity may be lacking in this system. However, whether it is possible to gain some temporal benefits by delaying the sowing time of one of the component crops without adversely affecting its productivity has not yet being investigated. Thus, there may be a need to differ the sowing dates of these intercrop combinations in order to investigate whether or not temporal complementarity between these component crops in an intercrop as regards radiation exist.

Partitioning of radiation interception among component crops in an intercrop

The partitioning of radiation interception by each component crop species in an intercrop is difficult and is usually subject to large sampling errors (Willey, 1990; Tsubo and Walker, 2002; Awal *et al.*, 2006). In any case, this largely depends on k (Sinoquet *et al.*, 2000). Several models for partitioning radiation interception by each component in an intercrop have been developed including those of Marshall and Willey (1983), Wallace *et al.* (1990), Wallace *et al.* (1991) and Keating and Carberry (1993) etc. It should be pointed out that the partitioning of light interception by each component is only feasible when the component crops are segregated into distinct categories such as where there is a distinct vertical stratification e.g. shrub/grass intercrops (Willey, 1990; Sinoquet *et al.*, 2000; Azam-Ali and Squire, 2002). However, Awal *et al.* (2006) observed that the partition of radiation based on the vertical differences might underestimate the true productivity because the interception of radiation is independent of the stand height (see Wallace *et al.*, 1991; Tsubo and Walker, 2002). In any case, where there is horizontal stratification as in the row intercropping of millet/groundnut studied by Marshall and Willey (1983) partitioning of light interception may also be possible. Marshall and Willey (1983) separated the

light intercepted by each component crop species and their study is widely cited by most workers of radiation in intercropping. They found out that millet in the intercrops intercepted 112% more PAR in the intercrop than in its equivalent sole crops. In contrast, groundnut intercepted 27% less PAR than its comparable sole crops. They argued that the improved groundnut efficiency was partly due to the greater efficiency of the C₃ canopy at lower light intensities, and perhaps partly the avoidance of light saturation of upper leaves.

It should be emphasised that it may not be possible to partition the radiation interception by component crops in an intercrop where the canopy foliage of the component crops intermingle (Awal *et al.*, 2006). That is, where there is no distinct canopy for each of the component crop. Sinoquet *et al.* (2000) explained this stating that because Beer's law deals with light transmission (i.e. non-intercepted radiation), it cannot be used by itself to estimate light sharing between the component crops, except if the canopies are segregated. Wheat/bean intercropping system do not exhibit the ideal canopy strata for measuring the light captured by each of the component crop, going by previous works (e.g. Hongo, 1995; Haymes and Lee, 1999).

Radiation use efficiency

Radiation use efficiency (RUE) is the ability of a crop to produce dry matter per unit of radiation intercepted and/or absorbed (Monteith, 1977; Awal and Ikeda, 2003; Lecoq and Ney, 2003). Other investigators computed the RUE as the ratio of the crop total biomass produced to the total PAR intercepted and/or absorbed by the crop (Tsubo *et al.*, 2001; Kindred and Gooding, 2005; Jahansooz *et al.*, 2007; Ruiz and Bertero, 2008). RUE was also defined as the slope of the relationship between the accumulated biomass and cumulative radiation intercepted and/or absorbed by the crop canopy (Rodrigo *et al.*, 2001; O'Connell *et al.*, 2004; Shearman *et al.*, 2005; Carretero *et al.*, 2010). RUE describes how efficient intercepted radiation was

converted to biomass (Biscoe and Gallagher, 1978; Robertson *et al.*, 2001). In general, RUE is conservative over a wide range of environment for a given crop species, provided the environmental conditions for growth are not limiting (Gallagher and Biscoe, 1978a; Zhang *et al.*, 2008). However, Bonhomme (2000) pointed out that the comparison of RUE data must take into consideration whether the computation was made using PAR or total solar radiation and especially whether radiation was absorbed or intercepted. Henceforth, in this paper unless otherwise stated RUE refers to the efficiency of conversion of intercepted PAR (Note that for convenience it is presented simply as RUE (g/MJ). The average RUE for a wide range of crop species was reported to be between 0.85 and 3.0 g/MJ for C₃ species and up to 4.8 g/MJ for C₄ species (Kiniry *et al.*, 1989; Prince, 1991 cited in Awal and Ikeda, 2003; Ruimy cited in Awal and Ikeda, 2003). Indeed, Kiniry *et al.* (1989) indicated RUE ranging from 1.2-2.93 g/MJ for a wide range of environment, with a mean RUE value of 2.8 g/MJ for well-managed wheat. Yunusa *et al.* (1993) also found mean wheat RUE value of about 2.93 g/MJ. Similarly, more recently Olesen *et al.* (2002) and Giunta *et al.* (2009) respectively reported RUE values in the range 1.8-4.2 g/MJ and 2.06-2.90 g/MJ.

Although it was pointed out earlier that RUE is conservative over a wide range of environment, several factors affect RUE. Awal and Ikeda (2003) stated that factors that affect RUE include photosynthesis, respiration, photorespiration, sink strength (see Borrás *et al.*, 2004), source-sink interactions (Reynolds *et al.*, 2007) and transport of assimilates. Other factors that affect RUE include crop species or cultivars involved, crop development stage (Bonhomme, 2000; Shearman *et al.*, 2005), vapour pressure and drought (Ridao *et al.*, 1996). RUE is also known to be limited by low temperature (Awal and Ikeda, 2003), nutrient availability especially N status, and N fertilization (Awal and Ikeda, 2003). RUE is also limited by leaf chlorophyll concentration, shading, plant density, sowing date,

location and intercropping (Sinclair and Muchow, 1999).

Radiation use efficiency in intercropping

As well as intercepting more radiation, intercropping has been shown to be more efficient than sole cropping in RUE (e.g. Marshall and Willey, 1983). However, with respect to intercropping, the RUE is sometimes estimated for the whole system (see Willey, 1990; Tsubo *et al.*, 2001). Tsubo *et al.* (2001) asserted that in intercropping situations, it would be more tenable to use the energy-based RUE since energy is a universal gauge of measuring biological productivity. Willey (1979a) asserted that if there is better spatial use of radiation by intercropping, this must have been achieved through more efficient use of radiation rather than greater radiation interception. Indeed, Willey (1990) in his study concluded that the light capture that would have been required to produce actual intercropping yields at sole crop efficiencies was 30% more than actual light; suggesting that RUE must have been improved by 30% in intercropping system. Awal *et al.* (2006) also stated that mean RUE of intercropped groundnut (2.13 g/MJ) was 79% higher than that of groundnut sole crop in their study. They added, that the RUE of combined intercrop (3.03 g/MJ) was more than two-folds that of sole groundnut but slightly lower than that of maize grown alone (3.27 g/MJ). According to them, the higher RUE of intercrop groundnut can also be explained by its low k value, which suggests that the canopy intercepted less PAR per unit dry matter produced, thus enhancing the RUE. Similarly, other investigations showed that the RUE of intercrop groundnut has been demonstrated to be enhanced when grown with millet (Marshall and Willey, 1983) and sorghum (Harris *et al.*, 1987). Hongo (1995) demonstrated that the total intercrop intercepted more radiation than both wheat and bean sole crops, but bean had lower RUE than wheat. However, earlier Asamoah-appiah (1988) investigation indicates that intercropping failed to improve RUE. The fact that there are contradictory results concerning RUE by

the intercrops relative to the sole crops suggests that there is still a gap of knowledge that needs to be filled to further clarify the pattern of RUE in intercropping.

Azam-Ali and Squire (2002) argued that sometimes it would be necessary to estimate the energy equivalent values of the lipid, protein and carbohydrate fractions in order to adjust total biomass especially where the component crop species differ in the lipid fraction. This is because not all plant organs have the same energy content per unit dry weight. These authors stressed that it is assumed that carbohydrate and protein has the same energy value in contrast to the lipid fractions. Thus, when such conversions are done the total biological output of a sole crop or intercrop system can be calculated in terms of mega joules (MJ). The novelty of this approach is that MJ are the same unit used to calculate the interception of radiation (Azam-Ali and Squire, 2002). However, clearly, when an oil seed crop is not one of the component crops intercropped such conversions are less necessary. Neither wheat nor bean is an oil seed crop; therefore, this approach is not necessary as regards wheat/bean intercropping system.

Partitioning of radiation use efficiency amongst component crops in an intercrop

It is very difficult to estimate the RUE of each component of an intercrop. This is because the canopies may be separate or intermingled. In situations where the canopy is either horizontally or vertically stratified the procedures used by Marshall and Willey (1983) may be worthwhile. In such cases, it is possible to use measurements of intercepted radiation and biomass to calculate the value of RUE for each of the component crops in the intercrop compared with its sole counterpart (e.g. Marshall and Willey, 1983). As stated earlier, Marshall and Willey (1983) explained the advantage of the intercropping by a 46% increase in RUE of the groundnut component combined with a 10% increase in the intercepted radiation by the millet component with little change to its RUE. However, the literature

overall tends to show that where the canopy is not stratified completely it would be better to calculate RUE for the whole intercrop by dividing the total biomass of all the components by the total amounts of radiation intercepted by the complete system (Azam-Ali and Squire, 2002). Going by previous investigations wheat/bean intercropping system do not appear to have the ideal canopy structure that would necessitates the computation of RUE for each of the component crop (Hongo, 1995; Haymes and Lee, 1999). In other words, for this intercrop combination the computation of RUE for the whole system may be more valid.

Conclusion

This paper clearly indicates the importance of both intercepted PAR and RUE for growth and yield of crops and intercrops. As was reviewed here, despite the increasing attention given to wheat/bean intercropping system research, only a few studies assessed these variables. Here it was concluded that there might be a need to assess both PAR interception and RUE in addition to any other parameters assessed in wheat/bean intercropping system if the physiological basis of intercrop productivity were to be well understood.

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